COMPARATIVE ANATOMY OF THE LEAF-BEARING CACTACEAE, IX

THE XYLEM OF PERESKIA GRANDIFOLIA AND PERESKIA BLEO

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THE TWO SPECIES OF *Pereskia* treated in this paper, *P. grandifolia* Haw. and *P. bleo* DC., have been considered to be closely related, the former occurring in Brazil and the latter in northwestern South America and Panama. It is of interest in this connection that Dr. Rodríguez reports (personal communication) that trees closely resembling *P. bleo* occur in dense forests at elevations of 1400 meters in Costa Rica. He is convinced that these trees, now growing in the wild, do not belong to a species which was originally introduced by man and subsequently escaped from cultivation.

These putative species, which may ultimately prove to be geographical races of a single species, are woody shrubs or small trees which may attain a height of five to seven meters at maturity. When growing in isolation they tend to form a single main stem or trunk which may attain a diameter of ten centimeters or more. However, as in the case of other leaf-bearing cacti their form may be modified by close crowding in hedges and by pruning or other mutilation by man.

The xylem of *Pereskia grandifolia* and *P. bleo* exhibits similar ranges of anatomical variability, which in turn closely resemble those that occur in the xylem of *P. sacharosa* Griseb. (Bailey, 1962). The vessels occur singly and in small clusters (FIGS. 1–8). Although commonly diffusely distributed, particularly in the first-formed secondary xylem, the vessels may at times be aggregated into more or less conspicuous zonal or concentric patterns (FIGS. 1, 2, 3). However, in some cases appearances of zonation are due solely to varying intensities of lignification in the thick secondary walls of the libriform fibers (FIG. 8). The libriform fibers which may be septate or nonseptate function in the storage of starch. The wood parenchyma is scanty paratracheal (FIGS. 5–8).

The abundance and width of the multiseriate rays, as seen in transverse sections of stems and roots (FIGS. 1–4), are highly variable, those of the roots tending to broaden more precociously and extensively than those of the stem, as in *Pereskia sacharosa*. The particular structural details (illustrated in FIGS. 1 and 2) of *P. grandifolia* and (FIGS. 3 and 4) of *P. bleo* do not provide reliable diagnostic criteria for differentiating the

two species, for each form of anatomical structure occurs in either species when numerous stems and roots of each species are examined. In fact, they may be more or less closely duplicated in the ranges of structural variability of *P. sacharosa*.

As in certain of the larger young stems of *Pereskia sacharosa* (Bailey, 1962), comparable stems of *P. grandifolia* (Fig. 7), and *P. bleo* (Fig. 5), exhibit evidences of lateral expansion of the parenchymatous, interfascicular parts of the eustele by cell enlargement during later stages in the maturation of the primary body, thus facilitating increase in the diameter of the pith. Owing to the broadening of the interfascicular parts of the eustele and retardation in the initiation of cambial activity within them, the first-formed parts of the multiseriate rays tend to be broader than in their subsequent extensions outward. However, the first-formed parts of the rays are lignified and their cells are in normal radial seriation, differing markedly from those in the basal parts of the trunks of *P. conzattii* Britt. & Rose, *P. autumnalis* (Eichlam) Rose, and *P. nicoyana* Web. (Bailey, 1963), where they are unlignified and their cells exhibit a conspicuous capacity for transverse enlargement. In other words, the pereskias of southern Mexico and Central America exhibit exaggerated ontogenetic and phylogenetic modifications in their multiseriate rays which facilitate greatly prolonged increase in the diameter of the pith.

In *Pereskia grandifolia* and *P. bleo*, as in *P. sacharosa* and in many other dicotyledonous shrubs and trees, the first-formed multiseriate rays in close proximity to the primary body tend to be vertically extensive. These rays sooner or later become dissected into lower rays (Figs. 9–12) which become laterally displaced in the outer secondary xylem during increase in the circumference of the cambium. During the outward extension of the rays, their cells become more or less conspicuously modified in size, form, and orientation. In the first-formed part of the rays, at least in some stems, the cells tend to be more or less vertically elongated or "erect" whereas in subsequently formed parts of the rays they become more nearly isodiametric or radially elongated, i.e. "procumbent." At times the rays, as in *Pereskia sacharosa*, may have more or less numerous erect cells along their sides and margins (Figs. 9 and 11). In outer secondary xylem, the rays of roots (Figs. 10 and 12) usually are conspicuously broader than in comparable secondary xylem of stems (Figs. 9 and 11).

In *Pereskia grandifolia* and *P. bleo*, as in *P. sacharosa*, the multiseriate rays of the stem have lignified secondary walls throughout their extension. They commonly contain more or less abundant starch. When crystals of calcium oxalate occur within them, they occur singly or as a few independent ones; aggregation into druses, such as occur characteristically in the unlignified parts of the multiseriate rays of *P. aculeata* Mill. (Bailey, 1962) and *P. conzattii* (Bailey, 1963), being absent.

The multiseriate rays in roots of *Pereskia grandifolia* and *P. bleo*, as in the roots of *P. sacharosa*, commonly are lignified throughout. However, in some cases the innermost parts of the first-formed rays of the three

species are composed of parenchymatous cells having thin unlignified walls (FIG. 15). In the limited number of specimens available to me, these parts differ from the unlignified ray tissue of *P. aculeata* and the unlignified parenchyma in roots of the Andean pereskias in being devoid of druses of calcium oxalate. The cells contain little if any starch but are packed with isotropic granular contents. The granules which vary considerably in size and form give a red color in Millon's reagent and a positive cytochemical coloration for protein in mercuric bromophenol blue (FIG. 16). For a description of the latter test see Mazia, Brewer and Alfert (1953). These tests suggest that the granules may be at least partly of proteinaceous composition.

It is of interest in this connection that Molisch (1885) found protein bodies of highly diversified forms in the parenchymatous cells of stems of *Epiphyllum*. He considered them to be reserve substances, whereas Chmielewsky (1887) subsequently concluded that they are products of excretion. However, the latter investigator agreed with Molisch that the protein bodies are formed in the protoplasm of living cells rather than in vacuoles or plastids.

In living cells of *Epiphyllum* the protein bodies occur in highly diversified forms of spindles, rings, and slender filaments variously contorted and aggregated. When sections containing living cells are transferred to hydrochloric, sulphuric, nitric, and acetic acids, ammonia, potassium hydroxide, or glycerin, the protein bodies are stated to contract, expanding laterally to form spheres which ultimately dissolve after more or less prolonged treatments. All of my specimens of stems and roots of *Pereskia*, *Pereskiopsis*, and *Quiabentia* were preserved by collectors in formalin-acetic-alcohol fixative. This raises the question whether the globular bodies illustrated (in FIG. 16) were derived during fixation from filamentous forms.

In sections of roots which contain globular bodies in the first-formed unlignified cells of the multiseriate rays many of the vessels in the xylem contain filamentous forms of protein bodies. They also occur in vessels of the stems of *Pereskia sacharosa*, *P. grandifolia*, *P. bleo*, and *P. tampicana* Web. The more slender filaments which grade down to less than half a micron in diameter may be diffusely distributed in the lumen of a vessel (center of FIG. 13) or aggregated in compact masses (FIG. 13, lower left and upper right). These filaments and their aggregations resemble those that occur in living cells of *Epiphyllum* (Molisch, figs. 3 and 5). In *Epiphyllum* the individual filaments may attain a length of 2.4 millimeters, but are variously contorted within the confines of a single cell. In my material individual threads commonly attain equivalent lengths but pass longitudinally through the lumina of a number of contiguous vessel members. Short, broad, spindle-shaped bodies of the forms illustrated by Molisch (figs. 1 and 4) are of relatively infrequent occurrence in vessels, but coarse strands of varying diameter are frequently present (FIG. 14 center). Such strands up to 10 micra in diameter may at times extend longitudinally in the lumen of a vessel for a distance of

more than two millimeters. Granular forms of protein bodies are of infrequent occurrence in the vessels of *P. sacharosa*, *P. grandifolia*, *P. bleo* and *P. tampicana*, but may be present in parenchyma adjacent to vessels which contain filamentous forms. Furthermore, filamentous, stellate, and other forms of protein bodies occur in the phloem parenchyma of these four species of *Pereskia*. Such occurrences as these in different parts of a single transverse or longitudinal section make it difficult to conclude that the globular forms are necessarily due to changes that occurred during fixation in F.A.A. It should be noted in this connection that Chmielewsky found that the solubility of protein bodies of *Epiphyllum* in 10% NaCl is inhibited after prior fixation in alcohol.

In my extensive collections, filamentous forms of protein bodies do not occur in the vessels of other pereskias, nor in those of *Pereskiopsis* and *Quiabentia*.

CONCLUSIONS

Pereskia sacharosa, *P. grandifolia*, *P. bleo*, and *P. tampicana* form a group of species characterized by a constantly distinctive form of sclerenchyma in their secondary phloem (Bailey, 1961). A conclusion that this structural similarity is *not* due to parallel or convergent evolutionary changes in distantly related species is strengthened by evidence presented in this paper. The structure of the xylem is remarkably similar in the stem and roots of the four species, and the multiseriate rays exhibit much less conspicuous phylogenetic trends of specialization than in other pereskias. Furthermore, the occurrence of filamentous forms of protein bodies in the vessels of these four species appears to be an additional indication of relatively close genetic relationship.

Preliminary observations indicate that globular forms of proteinaceous bodies occur at times in the parenchyma of the xylem and phloem of other pereskias. The occurrence of protein bodies of diversified forms is of considerable significance from cytological, biochemical, and physiological, as well as purely taxonomic points of view. For example, are protein bodies formed by protoplasm, which persists during late stages of maturation of vessels or do they intrude into the lumina from jacketing parenchyma? More extensive and detailed investigations starting with living tissues will be initiated and reported upon in a subsequent paper of this series.

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EXPLANATION OF PLATES

PLATE I

FIGS. 1–4. Transverse sections of the secondary xylem, × 11. 1, Stem of *Pereskia grandifolia* [*Castellanos*]. 2, *The same*, root. 3, Stem of *P*. aff. *bleo* [*Rodríguez 640*]. 4, *The same*, root.

PLATE II

FIGS. 5, 6. Transverse sections of first-formed and outer secondary xylem of stems, × 34. 5, First-formed secondary xylem of *Pereskia bleo* [Atkins Gard.]. 6, Outer secondary xylem of *P*. aff. *bleo* [*Rodríguez*].
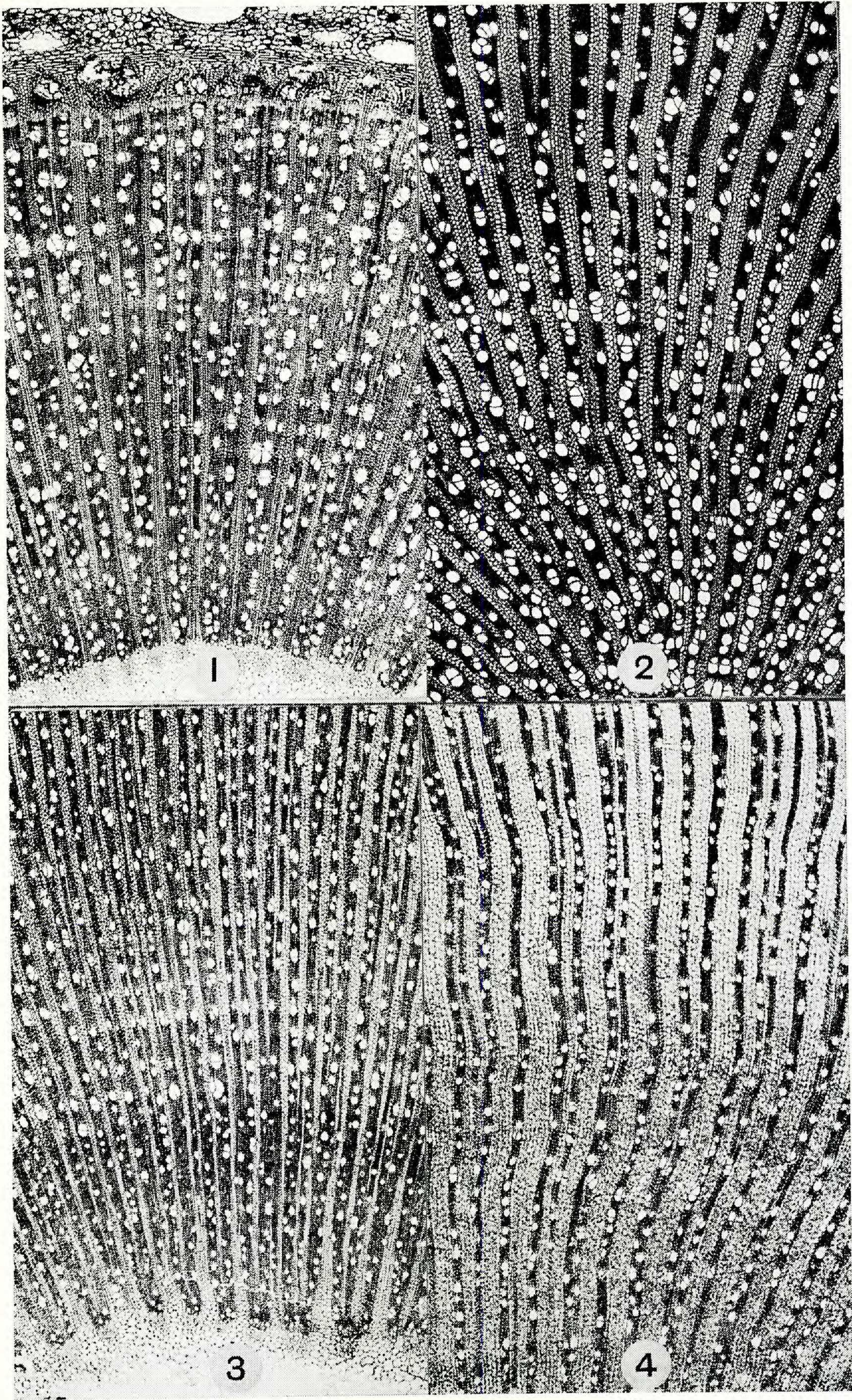
PLATE III

FIGS. 7, 8. Transverse sections of first-formed and outer secondary xylem of stems, × 34. 7, First-formed secondary xylem of *Pereskia grandifolia* [*Steyermark*]. 8, *The same*, outer secondary xylem showing zonation due to varying intensities of lignification.
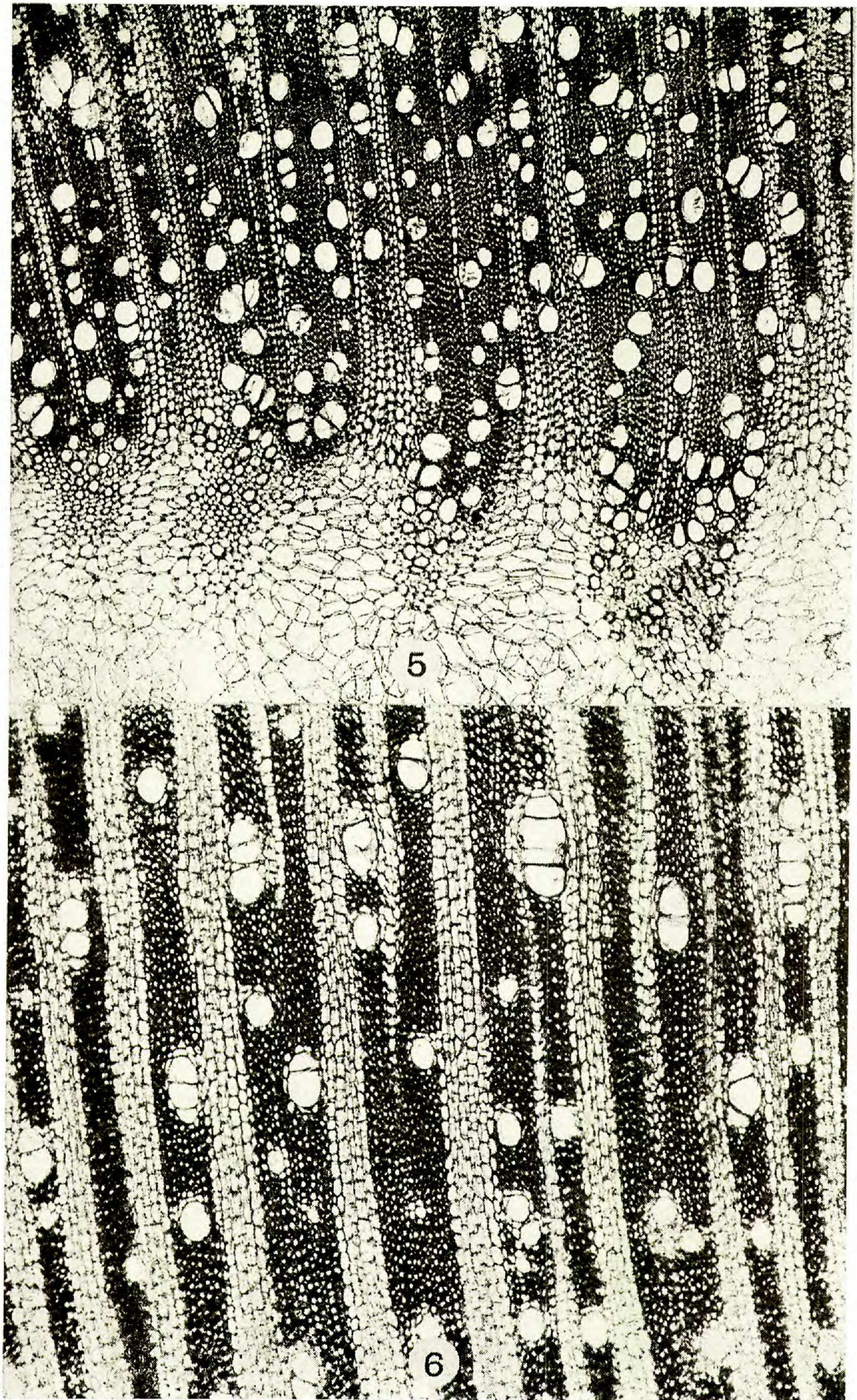
PLATE IV

FIGS. 9–12. Tangential longitudinal sections of secondary xylem, × 43. 9, Stem of *Pereskia* aff. *bleo* [*Rodríguez 640*]. 10, *The same*, root. 11, Stem of *P. grandifolia* [*Castellanos*]. 12, *The same*, root.
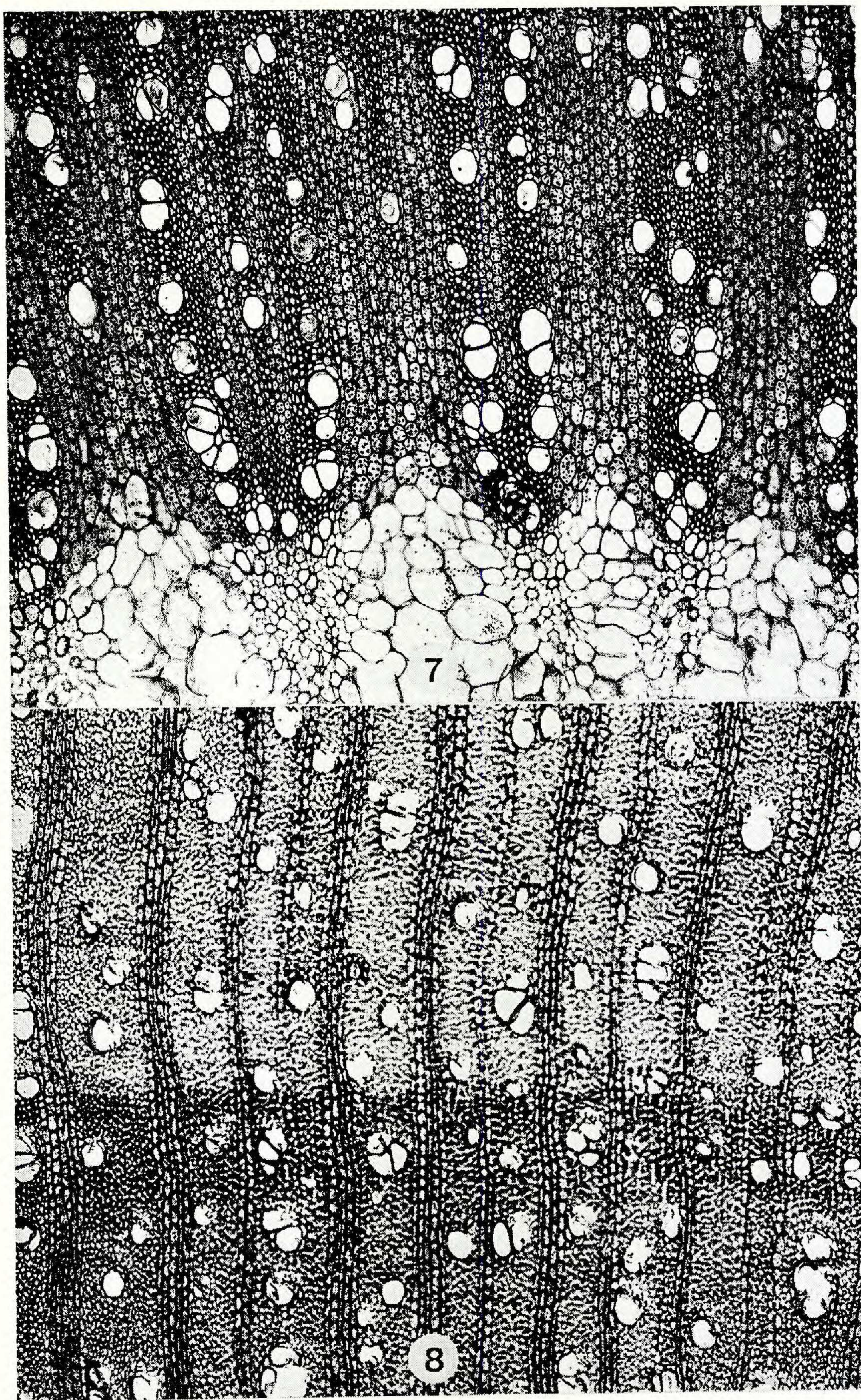
PLATE V

FIGS. 13–16. Longitudinal and transverse sections of stems and roots. 13, *Pereskia grandifolia* [*Castellanos*], longitudinal section of a stem showing slender filamentous forms of "protein bodies"; long individual filaments, center; compact aggregations of shorter filaments, lower left and upper right, × 510. 14, *The same*, showing coarser strands of "protein bodies," × 510. 15, *P*. aff. *sacharosa* [*Cárdenas*], transverse section of the central part of a root treated with phloroglucin-HCl, showing unlignified part (white) of first-formed multiseriate rays, × 34. 16, *P. grandifolia* [*Steyermark*], transverse section of the unlignified inner part of a multiseriate ray, showing granular forms of "protein bodies," × 510.
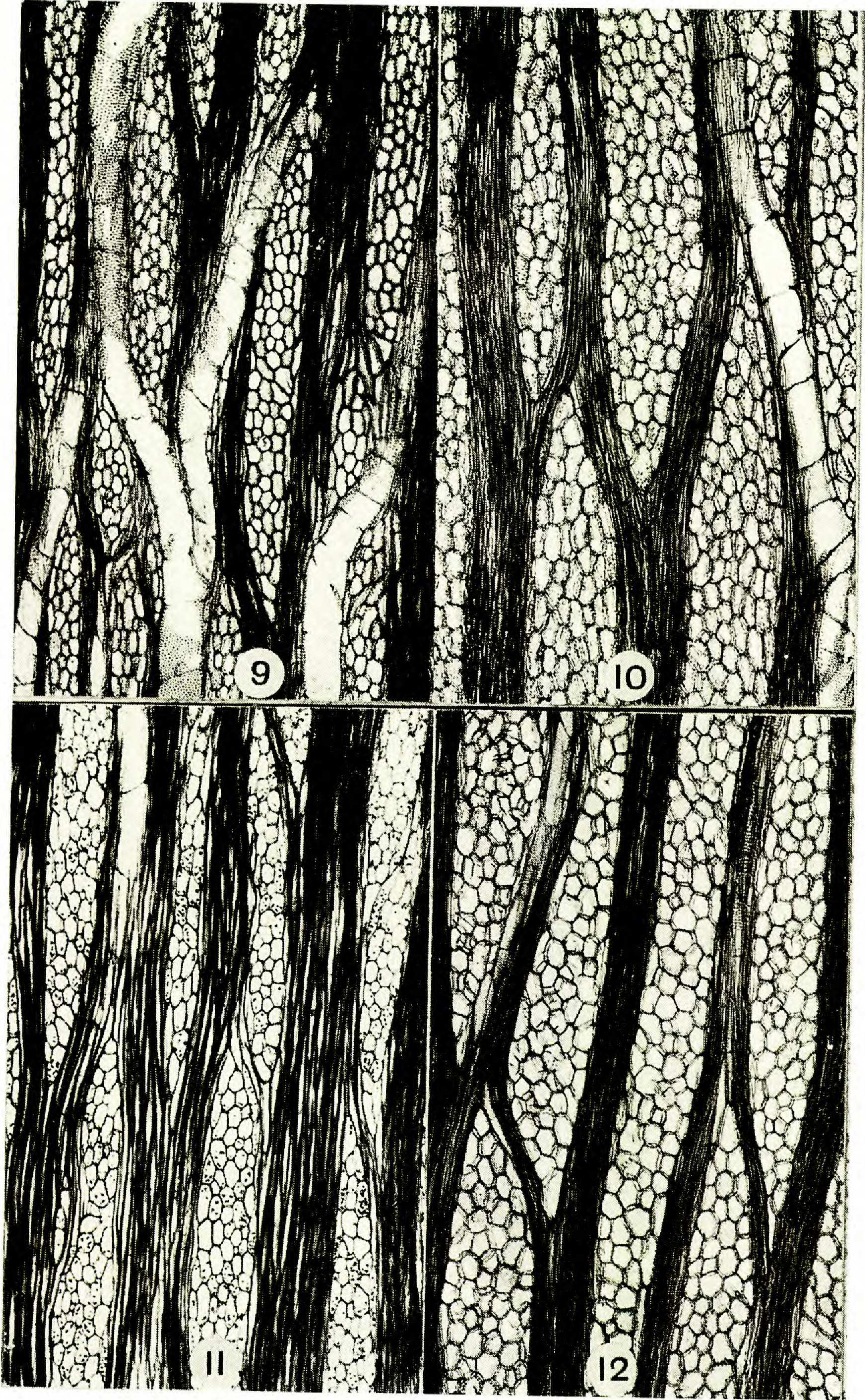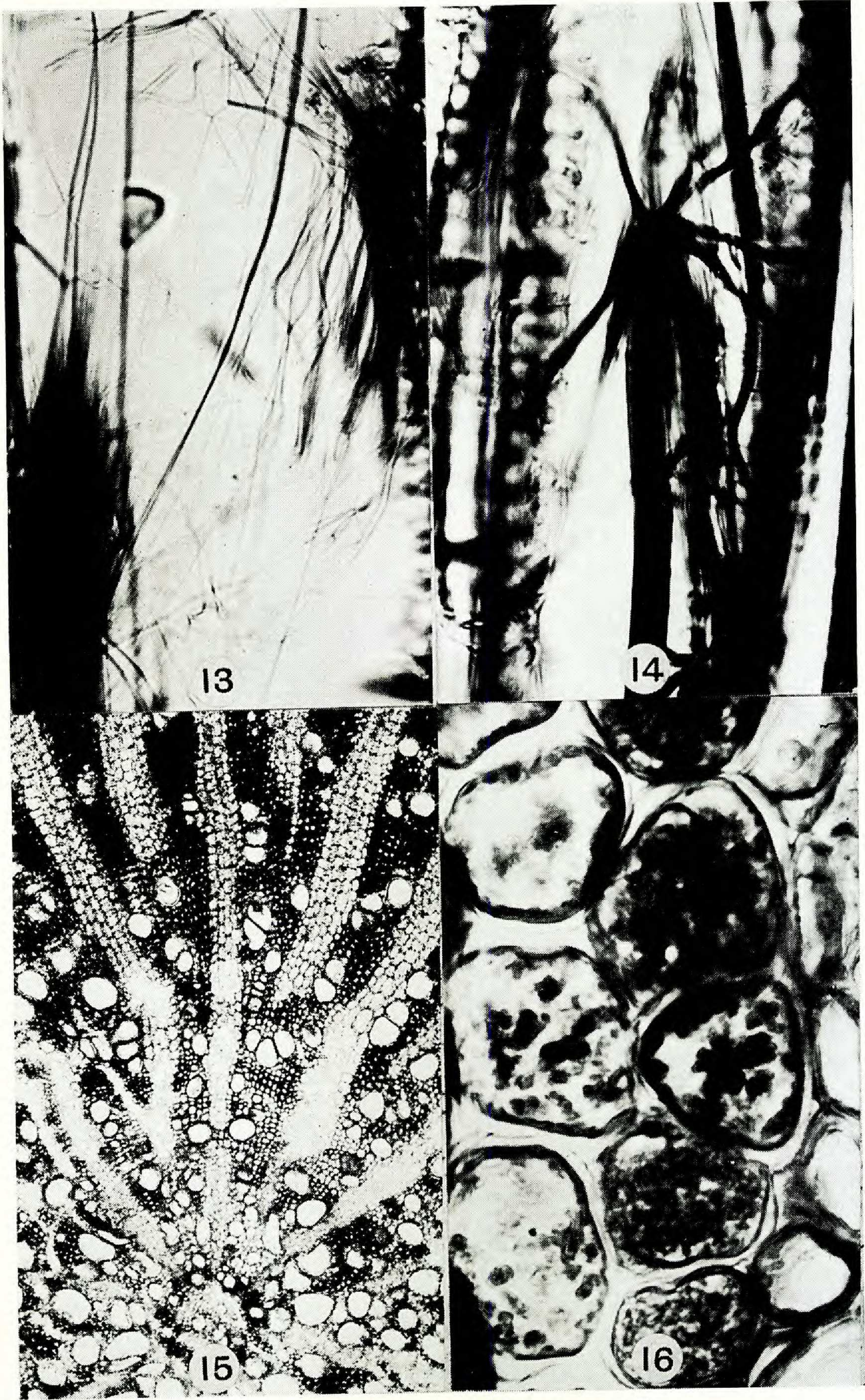
Plate I

BAILEY, LEAF-BEARING CACTACEAE, IX

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Plate V

BAILEY, LEAF-BEARING CACTACEAE, IX